一研 究 論 文一
Scientific Papers

Long-Term Diving Records of an Adult Female Northern Elephant Seal

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キタゾウアザラシの長期潜水記録

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要旨: 南極アザラシの冬季潜水行動を知るために開発した長期潜水記録計の現場実験を，回収が容易なキタゾウアザラシ (*Mirounga angustirostris*) を用いて行った．現場実験はキタゾウアザラシの連続的な深い潜水行動を知ることを主要な目的としてカリフォルニア，アニュ・ノエボ海岸で行った．1987 年 2 月繁殖終了後の雌の成獣に記録計を装着し，換毛のため再上陸した 5 月に記録計の回収を行い，潜水行動記録として初めて 73 日間におよぶ長期連続記録を得た．潜水回数は，73 日間 5024 回であり，1 時間平均 2.9 回の潜水を行った．全潜水の平均深度は 463.9±147 m であり，平均潜水時間は 17.1±3.4 分であつた．最大潜水深度と最大潜水時間は，934 m と 33.5 分であつた．最大潜水深度は実測された鰭脚類の深度としては最も深い記録であった．潜水は初めの 4 日間は深度を徐々に増し，500 m 深度に達すると安定した．しかし，潜水深度は昼夜で変わり，また約 20 日単位でも変化した．潜水時間は長期にも安定していた．ESI (Extended Surface Interval) 直後の潜水は非常に浅い潜水から再開され，数回の深度を増す潜水を経て通常の深度に達した．以上の実験の結果，本記録計は装着による動物行動への影響がないことが判明し，南極アザラシでも有効に利用できることがわかった．

Abstract: Seventy-three days long diving record of an adult female northern elephant seal (*Mirounga angustirostris*) was obtained using the long-term time depth recorder which was developed for Antarctic seal research by the National Institute of Polar Research, Tokyo. It was observed that the female northern elephant seal dived to a great depth continuously for a long period. It dived 5024 times during 73 days, 2.9 times per hour on the average. The mean dive depth and duration were 463.9±147 m and 17.1±3.4 min, the maximum values being 934 m and 33.5 min. The dive depth increased gradually on the first 4 days. After that, it fluctuated diurnally, while the dive duration remained rather stable. Following the extended surface intervals (ESIs: defined as surface intervals longer than 10 min) dives were shallow but the depth increased gradually.

1. Introduction

Study of diving behavior of seals and sea lions has progressed remarkably after new techniques were applied to the study. Especially, a technique of time depth recorder (TDR) has contributed to fill the gap in our knowledge on the diving behavior

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of pinnipeds. Diving behavior using the TDR was first measured on the Weddell seal (*Leptonychotes weddelli*) in Antarctica in 1970 (KOOYMAN, 1975). Thereafter, the same technique was applied to other seals and sea lions (KOOYMAN *et al.*, 1983; GENTRY *et al.*, 1986; GENTRY and KOOYMAN, 1986; KOOYMAN, 1986; KOOYMAN and TRILLMICH, 1986; KOOYMAN *et al.*, 1986), and the fundamental information, such as dive depth and duration, time spent in diving and on the surface, was brought out by the TDRs. The TDR technique was also adopted to the northern elephant seal (*Mirounga angustirostris*) since 1983. The first TDR was attached to the adult female seal at Año Nuevo Point, California in February 1983, and a free-ranging dive pattern for 11 days was obtained (LE BOEUF *et al.*, 1986). The second and third TDR experiments on the northern elephant seal were carried out at the same place in 1985 and 1986. The dive pattern for 14–27 days was obtained from the seven adult females as well (LE BOEUF *et al.*, 1988). These concentrated studies revealed a virtual aspect of the diving behavior of the female northern elephant seals, and also raised the new questions.

The above-mentioned experiments on the northern elephant seal gave the results that all seals began to dive as soon as they entered the water and made virtually continous deep dives throughout 14–27 days of the recording period. This diving performance is fundamentally different from that of other pinnipeds ever observed. LE BOEUF *et al.* (1988) discussed the continuity of deep diving from the viewpoint of feeding, predator avoidance and energy conservation. Then they concluded that metabolic depression is characteristic of diving in female northern elephant seals, and diving serves for resting and conservation of energy as well as feeding by day and night, and predator avoidance in shallow waters. However, they also pointed out that their current understanding of the physiological processes governing free-ranging dives derives from the examination of diving bouts of coastal species during their brief trips to the sea, and noted the necessity of modifications of explanation for the continuous diving in the pelagic elephant seal.

Based on the above situation we tentatively attached a long-term TDR to the adult female northern elephant seal to examine, a) durations of these continuous deep dives, and b) a long-term variability of diving parameters such as dive depth and duration. The long-term TDRs used in this study were develcped for Antarctic seal research and we tentatively used the TDRs for this experiment to examine effect of the TDRs on animals.

2. Method

Deployment of the long-term TDR (time-depth recorder) on the lactating female Yel that weighs 254 kg and is 235 cm in standard length was conducted after immobilization by ketamine and hydrochloride (BRIGGS *et al.*, 1975) at Año Neuvo Point, California on 16 February 1987. The attachment of the TDR was carried out applying the same epoxy technique as previously used in the 1985 and 1986 experiments (LE BOEUF *et al.*, 1988). The female left the site on 18 February and was sighted on Año Neuvo Island on 10 May. The TDR was recovered successfully.

The TDR used in the present study is 52 mm in diameter, 193 mm long, and weighs 980 g in air (Fig. 1). It is composed of three main parts: 1) recording paper

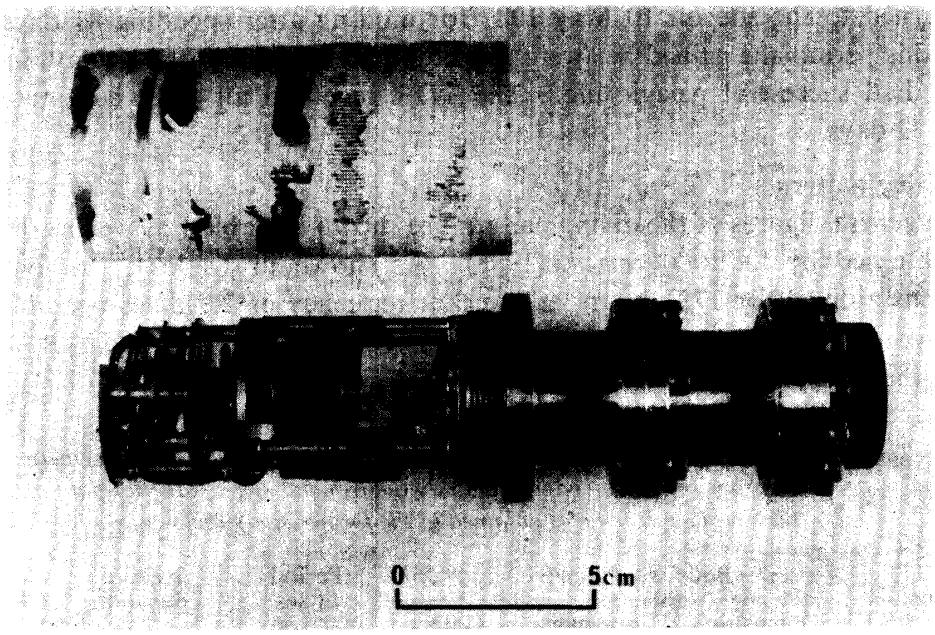

Fig. 1. Long-term time-depth recorder used in this study.

and stylus, 2) bellows-type pressure transducer, and 3) quartz paper drive motor and gear shifts. The recording paper is composed of 8.5 μ plastic base paper and carbon of 3.5 μ in thickness. Sharpness or angle of a diamond stylus is important to obtain a fine resolution line on the carbon-coated paper. When angle is too sharp, a stylus may break the paper and when it is not sharp, the line will be obscurely etched. The appropriate angle of stylus was determined to be 60 degrees by the test. Power of a quartz motor (DCM-6) was 1.6 g/cm: 1 rpm, and gear ratio was $1/30\times 1/60\times 1/12=1/21600$. Power consumption rate of quartz motor 110 μA. Accuracy of quartz timing was 15 s/month at 25°C. Thin carboncoated paper, 18 m long and 12 μ thick combined with a slow winding rate of 0.04 mm/min at the start and 0.06 mm/min at the end, made it possible to get a record of 130 days by shifting down the quartz motor. In this way, strong torque for winding the paper, with low power consumption, was achieved. A diamond stylus, connected to the pressure sensor, etched a thin high resolution line measuring less than 10 μ on the carbon-coated paper. The power source was two sets of 1.5 V alkaline batteries (UM-5). The bellows-type pressure sensor is highly accurate even after repeated increase in pressure and shows negligible mechanical hysteresis. The depth range of the TDR was 0–1000 m. As a casing material, strengthened aluminum was applied and TDR was strong enough against 3000 m water pressure.

The record on the carbon-coated paper was enlarged 17 times using a reader printer (Minolta RP507), and then it was digitized by computer. Dive measurements were calculated, stored on floppy disks and data booklet, and summarized by computer.

3. Results

The female seal left the breeding site on 18 February 1987 after weaning her pup and returned to the site on 10 May 1987 for molting after spending 81 days at sea. During this period she gained her weight 47 kg (increasing rate; 0.6 kg/day) indicating that she had successful pelagic life. The TDR recorded all dives continuously for the first 73 days.

3.1. Diving pattern

The general figures of the diving pattern are shown in Table 1 as well as the former result obtained by LE BOEUF *et al.* (1988). As shown in Table 1, the female seal continuously dived for 1721 hours at a mean frequency of 2.9 dives per hour. The mean dive depth and duration were 463.9±147 m (mean±S.D.) and 17.1±3.4 min. The maximum dive depth and duration were 934 m and 33.5 min.

Table 1. Summary of statistics from the diving records of an adult female northern elephant seal obtained in this study (above) and mean statistics data of the seven adult females obtained in the former study (below).

Subject	Body weight (kg)			Period at sea (days)	Record duration (hs)	No. of dives
	Departure	Return	Gain			
Yel	242 (16 Feb)	289 (12 May)	47	81	1721 (73 days)	5024
LE BOEUF *et al.* (1988)	322.5	399.0	76.5	72.6	318–619 (14–27 days)	819–1822

Subject	No. of dives/h	Record duration spent on surface (%)	Depth		Duration	
			max (m)	mean ±SD (m)	max (min)	mean ±SD (min)
Yel	2.9	17.0	934	463.9±147	33.5	17.1±3.4
LE BOEUF *et al.* (1988)	2.7	14.5	822	400 ±156	37.4	19.2±4.3

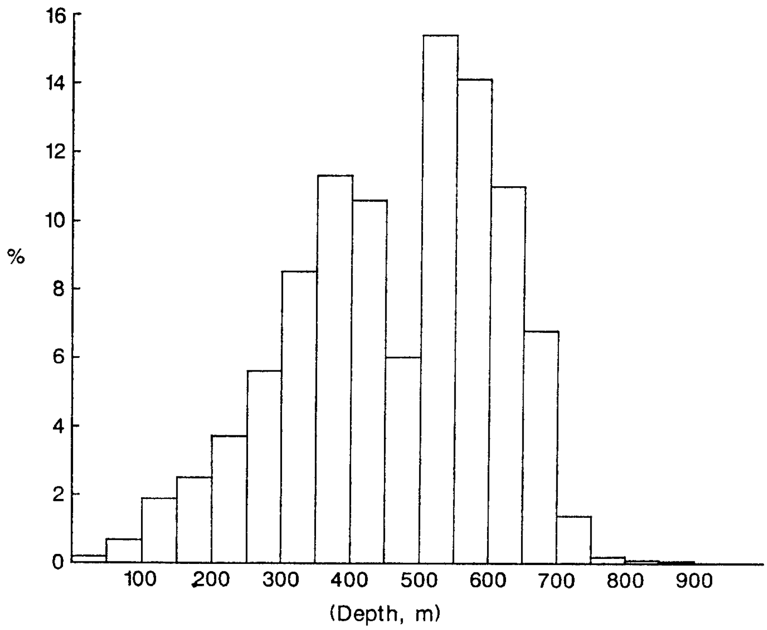

Fig. 2. Frequency distribution of dive depth in all dive records.

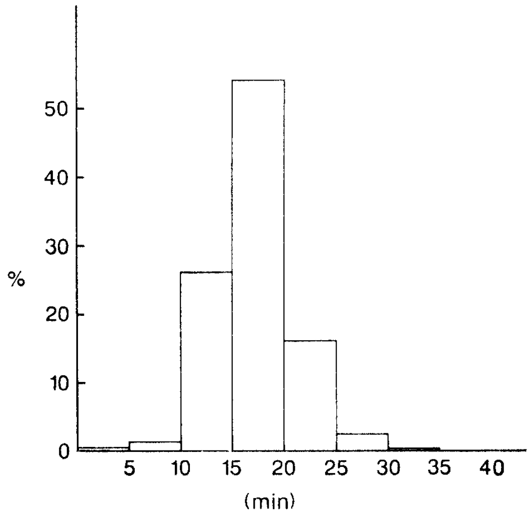

Fig. 3. Frequency distribution of dive durations in all dive records.

A frequency analysis of dive depth (Fig. 2) shows two modes, a peak at 350–400 m and another peak at 500–550 m. A frequency analysis of dive duration (Fig. 3) indicates that more than 95% dives were in a range from 10 to 25 min.

3.2. Long-term tendency of diving pattern

The long-term tendency of diving pattern of the female seal is shown in Fig. 4 which indicates that she increased her dive depth step by step during her pelagic life. We tentatively classified her diving performance into five stages by the depth as follows: On the first day of her entrance to sea, her dive depth did not exceed 200 m (stage 1). For the next three days or so, her dive depth exceeded 200 m but not 400 m (stage 2). The dive depth exceeded 400 m but not 500 m for 28 days (stage 3). The dive depth consistently exceeded 500 m for about 36 days (stage 4). In this stage her dive depth was very deep and stable. On the last 4 days, the dive depth decreased and seldom exceeded 600 m (stage 5).

The diving pattern of stages 1–5 is shown in Table 2. The record duration, number of dives, maximum depth, mean depth and maximum duration increased remarkably as the stage progresses except the last stage. On the contrary, record duration spent on the surface show a decreasing tendency. Meanwhile, the number of dives per hour and the mean duration do not show any marked differences.

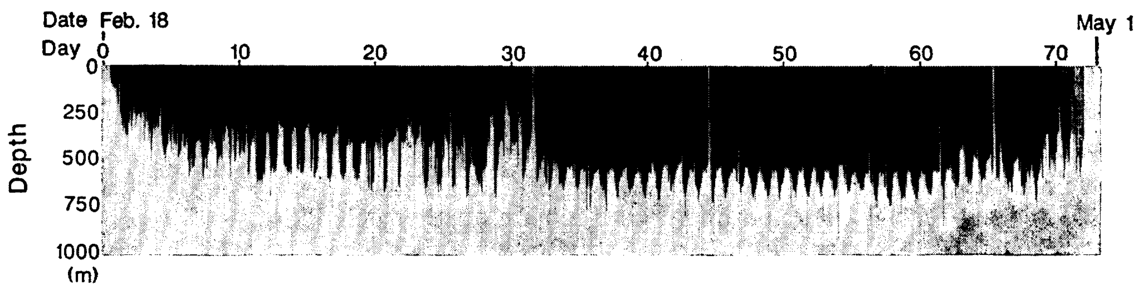

Fig. 4. All 5024 diving records of a female northern elephant seal showing a long-term tendency of dive depth. Each dive is represented by vertical component.

Table 2. Summary of statistics from the diving records of each diving stage.

Subject	Record duration (h)	No. of dives	No. of dives/h	Record duration spent in surface (%)	Depth max. (m)	Depth mean ±SD (m)	Duration max. (min)	Duration mean ±SD (min)
Stage 1	18:57	73	3.8	27.5	295	103.2± 42.6	16.9	11.3±2.7
2	64:32	183	2.8	25.7	525	261.3± 72.8	25.8	15.7±2.8
3	672:07	1936	2.9	18.5	720	400.0±125.5	28.9	17.0±3.6
4	864:12	2607	3.0	15.8	934	543.0±107.2	33.5	17.3±3.1
5	100:21	225	2.2	10.3	617	376.8±136.1	33.0	17.9±4.5

3.3. Extended surface time

As seen in Fig. 4, during 73 days of continuous diving, the female seal had a number of extended surface intervals (ESIs) which was defined as surface intervals longer than 10 min (LE BOEUF *et al.*, 1988). The ESIs in each stage are summarized in Table 3. The ESIs occurred 50 times during 73 days of her marine life and the frequency rate of ESIs (the number of ESI per dive) was very high at the beginning of dive life (stages 1 and 2) and lowered thereafter. On the contrary, the mean duration of ESI and the maximum duration of ESIs showed a tendency to increase as the stage advances.

Table 3. Summary of statistics from the extended surface intervals of each diving stage.

Subject	Record duration (h)	No. of ESI	No. of dives	Total duration of ESI (min)	Mean duration of ESI (min)	No. of ESI / Dives	Max. duration of ESI (min)	Min. duration of ESI (min)
Stage 1	18:57	2	73	21.7	10.85	0.0274	10.9	10.8
2	64:32	5	183	77.1	15.42	0.0273	24.2	11.2
3	672:07	16	1936	727.9	45.49	0.0083	264.0	15.6
4	864:12	25	2607	1570.9	62.83	0.0096	317.5	10.2
5	100:21	2	225	115.0	57.50	0.0089	57.8	57.2
	1721	50	5024	3547.6				

To understand the role of ESIs in the long-term consistent diving, the dive depth before and after ESIs was examined. As seen in Fig. 5, after a certain period of ESIs, the female elephant seal started her shallow dives and returned to the usual depth after a few dives. The profile of these shallow dives agreed with the C-type dives classified by LE BOEUF *et al.* (1988). The seal gained dive depth slowly to a certain depth.

4. Discussion

The long-term TDR experiment on a female northern elephant seal was conducted to examine the mode of continuous deep diving. As a result, we obtained the record of 73 days of long continuous dive, which is 2.7 times the past record on the same species (LE BOEUF *et al.*, 1988, Fig. 4). Our result differs little from the former one in diving performances such as the dive frequency (the number of dives per hour), the

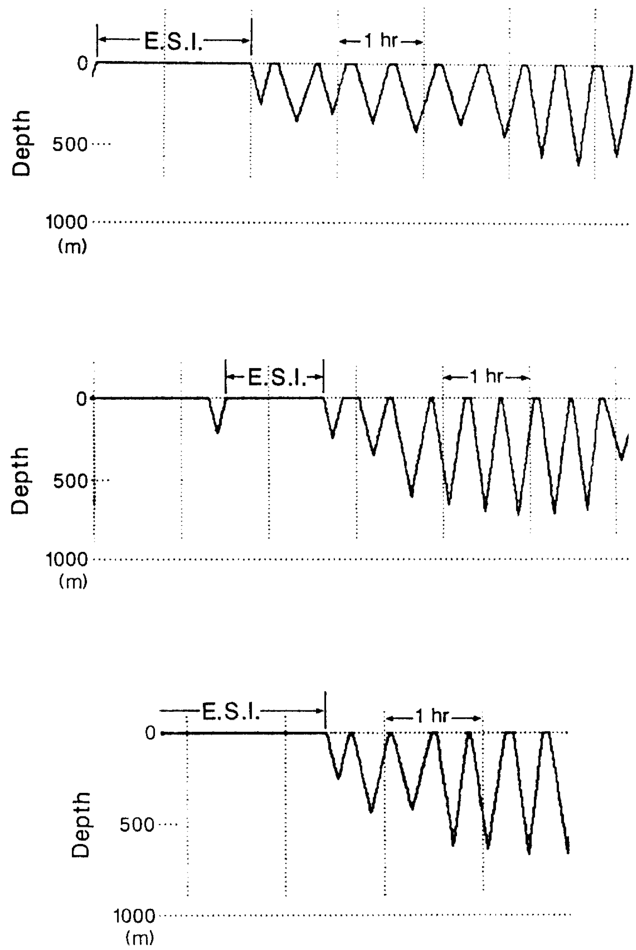

Fig. 5. The seal increased her dive depth gradually following the extended surface intervals (ESI). The figure is drawn by computer taking the maximum dive depth at the middle of duration of each dive.

time spent on the surface, the mean depth and the mean duration (Table 2). The experiment also indicated that deep continuous diving is not a short-term or transient behavior but is an invariant and characteristic behavior. This behavior is quite different from other diving animals (Table 4). However, when we examined the details of sequential processes of long continuous diving, it was found that the dive depth was variable and the dive duration was less variable (Fig. 4 and Table 2). As already indicated by LE BOEUF *et al.* (1988), the seal started her dives in the shallow continental shelf water and the dive depth increased gradually (stages 1 and 2). However, after these stages, the mean dive depth became variable in both daily and long-term basis. On the other hand, the mean duration was more stable even after stages 1 and 2 (Table 2). Daily change of the dive depth may be related to daily vertical migration of prey animals because the northern elephant seals feed in the deep layer of the mesopelagic zone and feed on squids and Pacific hake, *Merluccius productus* (CONDIT and LE BOEUF, 1984) that make nightly vertical migration. Daily change of the dive depth caused by daily vertical migration of prey species is often noticed in fur seals and penguins (GENTRY and KOOYMEN, 1986; CROXALL *et al.*, 1988; NAITO, unpublished). The cause of for the long-term change in dive depth is not clear, yet

Table 4. Dive bout duration, dive depth and dive duration of some pinnipeds and Adelie penguin (mean).

	Mean dive bout duration (h)	Mean dive depth (m)	Mean dive duration	Prey
Weddell seal (KOOYMAN, 1975; KOOYMAN *et al.*, 1979, 1980)	8–11	<200	—	Fish
Northern fur seal (GENTRY *et al.*, 1986)	2.2	68	2.2	Fish, squid (Ephipelagic, Demersal)
Antarctic fur seal (KOOYMAN *et al.*, 1986)	1.9	30	0.8–3.1	Krill
South African fur seal (GENTRY and KOOYMAN, 1986)	3.0	41–49	1.7–2.5	Shoaling surface fish, pelagic fish, squid
Galapagos fur seal (KOOYMAN and TRILLMICH, 1986)	2.9	26	2.4–7.7*	Pelagic squid, fish
Adelie penguin (NAITO, unpublished)	0.48	9.4	1.7	Krill

* Maximum data.

it is likely that the feeding ground shifts from one place to another different depth of water. The prey species may also shifted. Because as seen in Fig. 4 and Table 2, the mean dive depth is relatively constant within each stage. This may suggest that the seal stayed at the same feeding ground for a certain period and moved to another feeding ground and fed on different prey animals.

The mean dive duration seemed to be very consistent in stages 3–5 where the dive depth changed remarkably. This is a very clear contrast to the dive depth. At present, we cannot obtain any explanation for the relations of the above factors. Yet, it is possible that the dive duration is a more independent factor regulated by more complicated physiological conditions. LE BOEUF *et al.* (1988) examined the relation between the dive depth and the dive duration and suggested that the breakpoint or apparent change from one function to another was around 400 m. In this study, we found the breakpoint at same depth which may reflect a change between the daytime and the nighttime dives. However, what regulates the dive duration is not clear yet.

As already mentioned, the dive depth of this seal is variable and is determined mainly by the ecological factors such as feeding. However, a physiological factor of deep dive is also very important to elephant seals. It is very interesting to consider physiologically that the seal always began with a shallow dive and the dive depth gradually increased after extended surface intervals (ESIs) (Fig. 5). As indicated by LE BOEUF *et al.* (1988), the elephant seal dives at 1.35 m/s (the water pressure increases at a rate of 8.18 ATM/min), and a sudden exposure to greater pressure would induce tremor and convulsion. So, the seal might avoid such physiological irregularities by gradually increasing her dive depth. The same phenomenon was found in the initiation of dive bout of the Adelie penguin, *Pygoscelis adeliae* (NAITO, unpublished).

We tentatively examined the long-term TDR experiment on the female northern elephant seal and was able to know its continuous deep diving behavior. However, our results led us to only an entrance of the study. More diving information from different sexes and different age groups is required in order to understand the particular diving behavior of this seal.

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